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INVITED REVIEW

The ecology and evolution of induced responses to herbivory and how plants perceive risk

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Abstract. 1. Plants perceive herbivore damage or increased risk and respond. These changes may increase plant fitness, although effects on fitness have often been assumed without supporting evidence.

2. Three models have been proposed to explain induced rather than constitutive defence. The optimal defence model posits that induction allow plants to reduce allocation costs; it predicts demonstrably lower costs when defences are not needed. The moving target model posits that induction increases spatial and temporal variability; it predicts that variability will be difficult for herbivores and will provide defence. The information transfer model posits that induced responses provide cues to other tissues on that individual plant and to other organisms in the community; it predicts that induced cues will provide systemic resistance, deter herbivores, and/or attract enemies of herbivores, thereby benefiting the induced plant.

3. All three models predict that cues must be reliable to be useful. In some cases, cues provide specific information about the damaged plant tissue and the herbivore and this specific information may allow plants to fine-tune responses. Recent theory posits that selection should favour plants that minimise recognition errors and reduce fitness costs associated with errors.

4. Future research should focus on exploring different modalities used by plants to perceive herbivore risk, the benefits and costs of perceiving cues and inducing resistance, and the basic natural history of these phenomena. Induced responses have great unrealised potential in agriculture, and research should focus on host plant resistance rather than attempting to involve other trophic levels.

Key words. Communication, cues, defence, perception, priming, resistance.

Introduction

Entomologists have recognised for roughly 50 years that plants that are attacked by herbivores change in ways that defend their tissues and discourage subsequent feeding (e.g. Green & Ryan, 1972; Haukioja & Hakala, 1975). Many excellent reviews describe our current understanding of mechanisms by which plants perceive damage by herbivores, the signalling that occurs within a plant, and the chemical and morphological responses that are triggered (Howe & Jander, 2008; Mithöfer & Boland, 2012; Kant *et al.,* 2015; Schuman & Baldwin, 2016). This review will focus instead on the ecological phenomena that make up induced responses to herbivory, a subject that has been less emphasised in the more mechanistic treatments cited earlier (although see Kant *et al.,* 2015, and Erb, 2018). I will consider the following questions: what is induced resistance and why do plants employ it; how do plants perceive that they are at risk of herbivory; which cues provide the most reliable information; what are the consequences of responding or not responding to cues; what would we like to know in order to move forward in understanding induced responses to herbivory?

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Induced responses to herbivory

When plants are damaged by herbivores, they change in many ways and some of these 'induced responses' provide 'induced resistance' to subsequent exploitation by herbivores (Karban & Myers, 1989). While induced resistance has been found to be ubiquitous, 'induced defences', which increase plant fitness

under conditions of high risk of herbivory, have only been demonstrated infrequently. The connection between reductions in the performance of herbivores and benefits to plants has often been implicit (see Hare, 2011; Erb, 2018), although a limited number of studies have found compelling evidence for this link (e.g. Agrawal, 1998 for direct defences; Schuman *et al.,* 2012 for indirect defences that involve predators of herbivores). As herbivores often compensate for lower-quality food by consuming more of it and parasitised herbivores often continue to feed and damage their hosts, this link should not necessarily be assumed; this situation presents a difficult problem for empirical biologists, although an examination of herbivore behaviour may be helpful in extrapolating effects of induced resistance to effects on plant performance when plant fitness is difficult or impossible to measure (Karban, 2011).

Why induced resistance?

Induced responses that are only expressed after a plant has perceived an increased risk of attack have been well documented. They leave the plant potentially vulnerable to herbivory if the plant fails to correctly evaluate the risk it is facing, fails to choose an appropriate response, or is unable to protect itself before the herbivore has consumed enough plant tissue to reduce its fitness (Karban & Orrock, 2018). These difficulties beg the question: why has induced resistance evolved rather than constitutive resistance which is always expressed?

Three classes of explanations have been proposed that favour induced defences (Table 1; following Kessler, 2015). Below I summarise each of these, highlight their unique predictions, and evaluate the evidence supporting these predictions. Although they emphasise different selective forces and make different predictions, these hypotheses are not mutually exclusive and all three may operate in many situations.

Defence is costly – optimal defence theory

The oldest and best-studied explanation for induced defences is that defences are costly and plants can save these costs when defences are not needed (Rhoades, 1979; Karban, 2011). According to this scenario, defences are only expressed when risk of herbivory is high. This expectation is based on the assumption that plants face trade-offs between allocating valuable resources to defending against herbivores and allocating them to growing, reproducing, and/or other functions related to fitness. Under conditions of high risk, there are many examples of induced secondary plant metabolites providing effective resistance against herbivores. As the result of considerable research spanning decades, there are some compelling examples of trade-offs between defence and growth but also examples where this phenotypic trade-off is not seen: the evidence for costs of defences is still equivocal and context-dependent (for recent reviews see Cipollini *et al.,* 2014, Züst & Agrawal, 2017).

Three additional points about this hypothesis are worth noting. First, although there is growing evidence for costs of defence, these costs cannot generally be quantified in terms of resources allocated to particular functions and are often better represented by ecological costs (Cipollini *et al.,* 2014; Züst & Agrawal, 2017). Ecological costs can take the form of defences against one herbivore coming at the expense of another important function, such as defence against pathogens (Thaler *et al.,* 2002) or induced defences against herbivores reducing attractiveness to pollinators or other plant mutualists (Kessler *et al.*, 2011). Second, costs of defence may be further reduced by priming, i.e. by preparing to induce resistance without fully committing to gene expression (Engelberth *et al.*, 2004). Primed plants can react more quickly and more strongly although they experience little cost in the absence of actual herbivory. Empirical estimates of costs may be conservative as plant competition in natural settings is expected to exaggerate initial costs of induction (Douma *et al.,* 2017; de Vries *et al.,* 2019). Third, some authors have assumed that most plants exhibit priming rather than induced resistance involving full expression of genes for defensive traits. Although there are certainly convincing demonstrations of priming, it remains to be seen how many of the examples of induced responses actually involve priming.

Plant variability provides defence – the moving target model

A second potential mechanism of induced defence posits that variability *per se* can be defensive (Adler & Karban, 1994). Arguments about whether plants are 'induced'/'primed', or not, make the implicit assumption that the expression of particular defensive traits will necessarily protect plants against their herbivores better than uninduced plants. There are several

Table 1. A comparison of three models that attempt to explain induced plant defences.

	Optimal defence	Moving target	Information transfer
Main premise	Defence only when needed	Variability provides resistance	Information reduces damage by herbivores
Role of costs	Allocation costs are reduced, favouring induced defence	Costs do not drive the evolution of defence	Costs and benefits depend on responses of other species
Predicted pattern or signature	Costs reduced relative to constitutive defence	Induction increases spatial and temporal variability	Receivers and their responses determine fitness consequences
Evidence of effectiveness for plants	Induced secondary metabolites often effective but exceptions exist	Little evidence, few studies	Little evidence, few studies examine fitness
Commonly studied?	Yes	Few studies	Yes

problems with this assumption that induced resistance operates in this simple manner. First, traits that may provide induced defence against one herbivore species may render the plant more attractive or vulnerable to another herbivore (an ecological cost), i.e. defences depend on the ecological context. Second, induced responses are spatially localised; they increase the spatial and temporal variability of tissues within a plant and within a community.

Reduced costs are not predicted to necessarily favour induced resistance in this model. Instead, the key prediction is that induced plants will be more variable, making it difficult for herbivores to match their physiology with the primary and secondary metabolites of host plants (Adler & Karban, 1994; Pearse *et al.,* 2013a). Herbivores have physiological mechanisms that enable them to acclimate to the characteristics of their host plant tissues (Wetzel & Thaler, 2016). For example, insects metabolise secondary chemicals by producing detoxification enzymes, particularly cytochrome P450 s, when they encounter specific plant compounds (Despres *et al.,* 2007; Li *et al.,* 2007). Herbivores will be less effective at matching their detoxification enzymes to plant secondary chemicals if those chemicals change over time and space (Pearse *et al.,* 2013a).

This mechanism has received less attention than the simple allocation costs of optimal defence theory. A recent meta-analysis indicated that variability in plant nutrients is difficult for herbivores and reduces the value of plant tissue for them (Wetzel *et al.,* 2016). For example, gypsy moth caterpillars reared on more variable diets experienced reduced pupal mass and longer development compared with caterpillars reared on less variable diets but with the same mean level of nutrients (Stockhoff, 1993). In another study involving secondary chemicals, variability made it more difficult for herbivores to physiologically match their host defences (Pearse *et al.,* 2018). Cabbage looper caterpillars were fed diets that had the same mean level of furanocoumarins but differed in how variable those secondary plant chemicals were (constant levels versus fluctuating levels). Caterpillars on more variable diets experienced lower growth rates, longer development times, lower fecundity, and reduced population growth. Variability in constitutive metabolites can also be effective, although induced responses provide additional variability. Variability may reduce the benefits for herbivores without necessarily benefiting the plant if herbivores consume more lower-quality plant tissues. Traits that reduce host quality will provide more effective plant defence if herbivores choose to consume less of it. Few studies have examined the role of variability so it is not clear if this mechanism is common in nature. As such, this role of induced responses as a driver of variability for herbivores deserves more consideration.

Information transfer provides defence

When plants respond to actual herbivory or cues of elevated risk, these responses are 'public' information and may be perceived by other plant tissues on that same individual, other neighbouring plants, herbivores, and the predators and parasites of those herbivores (Stam *et al.,* 2014). Some of this public information may affect other tissues and/or other members of the community, thereby benefiting the emitter (Kessler, 2015). This information may provide ecological benefits through interactions with other species, analogous to the ecological costs discussed earlier. For example, when plants are damaged, they emit volatile cues that cause other tissues on that same individual to increase levels of resistance (Karban *et al.,* 2006; Frost *et al.,* 2007; Heil & Silva Bueno, 2007). Neighbouring individuals eavesdrop on these cues and adjust their own defences. These same changes provide information to other herbivores indicating that this plant tissue is already colonised by potential competitors and/or is well defended (or poorly defended), which may affect the likelihood of attack by herbivores arriving later (De Moraes *et al.,* 2001; Karban, 2011; Morrell & Kessler, 2017). Induced responses may also be perceived by the predators and parasites of herbivores and these species may protect the plant (e.g. Schuman *et al.,* 2012).

According to this hypothesis, allocation costs do not drive the evolution of induced resistance. Instead, the consequences of induced resistance are determined by the identities of species in the surrounding community that perceive and respond to the information that has been made available. In other words, ecological costs and benefits play a critical role. For example, the net effects of inducible glucosinolates in *Brassica nigra* depended on the neighboring plants and the available herbivores (Lankau & Strauss, 2008).

Like the previous hypothesis, this model is a possible mechanism for induced resistance and has received much less attention than optimal defence. While there are many examples of plant cues that affect levels of herbivore damage to neighbouring tissues and plants (reviewed by Karban *et al.,* 2014b) and plant cues that attract predators and parasites of herbivores (reviewed by Turlings & Erb, 2018), relatively few studies have documented an increase in plant fitness associated with this transfer of information.

Plants perceive herbivory via multiple modalities

All three models predict that plants will only respond to cues that indicate an elevated risk of attack. Actual herbivory is the most common trigger for induced resistance against herbivores (Karban, 2015). The presence of dislocated plant molecules and fragments of macromolecules from disrupted cells allows plants to recognise that their tissues have been damaged (Duran-Flores & Heil, 2016). These so called DAMPs (damage-associated molecular patterns) are sufficient in many systems to cause induced resistance following mechanical wounding. Plants also respond to molecules specifically from herbivores (herbivore-associated molecular patterns, or HAMPs) that the plants encounter during herbivore feeding or other activities (Acevedo *et al.,* 2015). Plants have been shown to perceive saliva, oral secretions, gut regurgitant, faeces, eggs, and oviposition accessories (see later). As these indirect cues are derived from herbivores, the herbivores or their associated microbes may also release 'effectors' that interfere with plant perception of HAMPS and the induced responses that could follow. The distinction between plant- and herbivore-derived cues is often vague; for example, legumes recognise inceptin, a catabolic plant product that has been broken down by enzymes from a feeding caterpillar (Schmelz *et al.,* 2006).

Plants most commonly respond to cues that have been released by their own damaged tissues, as opposed to those of other individuals (Karban *et al.,* 2006; Frost *et al.,* 2007; Heil & Silva Bueno, 2007). These cues may travel from cell to cell, through the vascular system of the plant, or through the gaseous headspace that connects plant tissues. Responding to 'self' cues allows plants to coordinate their own systemic defences, although it is unclear if selection has favoured plants that emit cues about damage.

Volatile cues that are emitted during damage allow nearby individuals to eavesdrop on neighbours and adjust their defences (Karban *et al.,* 2014b). The release of these cues may be the unintended consequence of their high volatility; in some instances this is clearly not the case, as HAMPs cause even undamaged portions of the plant to produce additional sources of cue (Turlings & Tumlinson, 1992; Dicke *et al.,* 1993). Physiological models also suggest that emission of some volatile cues involves active processes (Widhalm *et al.,* 2015). Herbivore-induced volatiles dissipate over relatively short distances, limiting the spatial extent of volatile communication. An additional limitation on volatile communications occurs because plants are likely to be more responsive to cues from their own damaged tissues compared with those of other individuals (Karban & Shiojiri, 2009; Pearse *et al.,* 2013b). Despite this limitation, plants of other species have been found to respond to volatile cues of heterospecific neighbours in a few instances (Farmer & Ryan, 1990; Karban *et al.,* 2000; Glinwood *et al.,* 2004).

Mycorrhizal fungi, which connect plant individuals of the same and different species, also serve as conduits for cues about herbivores (Gilbert & Johnson, 2017). Bean plants sharing hyphal connections with conspecifics that had been infested with aphids were more repellent to colonising aphids and more attractive to aphid parasitoids than unconnected controls, and these connected plants were as repellent as individuals that were actually infested with aphids (Babikova *et al.,* 2013). Similarly, cues from mechanically or caterpillar-wounded Douglas fir seedlings were passed to connected ponderosa pine seedlings and led to increased activity of putatively defensive enzymes (Song *et al.,* 2015).

Plants perceive indirect cues indicating risk of herbivory

In addition to cues that result from actual herbivory, plants sense and respond to many less direct cues. First, plants recognise cues that precede any actual feeding, such as insect footsteps that rupture trichomes and other tissues on the leaf surface (Hall *et al.,* 2004; Peiffer *et al.,* 2009). Similarly, plants recognise insect eggs and initiate defences before those eggs hatch and the insects begin feeding (Hilker & Fatouros, 2016). For example, when cabbage white butterflies place eggs on *Brassica* leaves, they inadvertently allow benzyl cyanide to contact the leaf; the plant recognises this chemical, causing changes that can kill the eggs, prime the plant to respond if the eggs successfully hatch, and ultimately result in more seed production compared with plants with experimentally added caterpillars but no eggs (Pashalidou *et al.,* 2015).

Second, plants recognise indirect cues that indicate feeding. These include cues from salivary glands and regurgitant from insect guts, and they have been described for many taxa, including caterpillars, crickets, grasshoppers, fruit flies, beetles, and aphids (Kant *et al.,* 2015). Plants also detect other chemical cues that indicate herbivore presence, such as frass from caterpillars (Ray *et al.,* 2016), mating pheromones of flies (Helms *et al.,* 2013), and kairomones (locomotion mucus) from snails (Orrock *et al.,* 2018). Recent experiments suggest that plants perceive and respond to acoustic vibrations caused by insect chewing (e.g. Appel & Cocroft, 2014). The plants in these experiments did not respond to wind or insect singing. The generality and significance of these exciting results need further study.

Reliability of cues

Selection will only favour plants that respond to reliable cues (Karban, 2011). If defences are costly, cues that lead to inappropriate responses will not increase plant fitness. Indeed, virtually all models of induced resistance assume that cues must be reliable for another organism to benefit by responding to the information, whether those receivers are other plants, as discussed here (e.g. Douma *et al.,* 2017), herbivores (e.g. Rubin *et al.,* 2015), or the predators and parasites of herbivores (e.g. Kessler & Heil, 2011). This high premium on reliability of cues has many consequences.

Damage to a plant's own tissues is likely to be the most reliable and informative source of information, and this is consistent with observations that damage to self is the most frequently documented cue eliciting plant responses (see earlier). As DAMPs are derived from the damaged plant, they may be more reliable cues than HAMPs, which are derived from other organisms. Although less reliable, HAMPs may provide specific information lacking in DAMPs.

In many instances, herbivores are able to alter cues with 'effectors' so that the cues either cannot be recognised by plants or provide misleading information. For example, many caterpillars cut the veins and petioles of host leaves before feeding, preventing the plant from transmitting signalling molecules and thereby recognising them (Dussourd, 2017). Microbes that herbivores carry may interfere with the transmission of plant cues (e.g. Frago *et al.,* 2017). In other cases, herbivores are able to make plants misidentify them as pathogens; the plants then mount a 'defence' against this inappropriate threat, thereby making the plant more susceptible to herbivory (e.g. Bruessow *et al.,* 2010).

Animal behaviourists have found that some individuals provide more reliable information about risk than others and that receivers respond more strongly to alarms emitted by these more reliable neighbours (Pollard, 2011; Couchoux *et al.,* 2018). Future work with plants should consider whether they also distinguish among the alarms of different individuals.

Specificity of cues

Cues that provide more specific information are likely to be more valuable to plants if those cues enable them to fine-tune their responses to the particular threat they are facing. The

timing and area of mechanical damage to bean leaves were both found to alter the volatiles that the leaves emitted (Mithofer *et al.,* 2005). These volatile cues resulted from the pattern of mechanical injury (DAMPs) and it is expected that cues elicited by herbivores (HAMPS such as saliva, faeces, and so on) will provide even more specific information, although evidence supporting this hypothesis is limited and difficult to interpret (Acevedo *et al.,* 2015; Duran-Flores & Heil, 2016). For example, specialist herbivores induced emission of fewer volatiles but in higher quantities than generalists, suggesting that cues could potentially provide herbivore-specific information (Rowen & Kaplan, 2016).

Volatile emissions have been found to vary depending upon the attacking herbivore (Rowen & Kaplan, 2016). For example, the volatiles emitted by *Brassica rapa* contained information that indicated the feeding mode of the herbivore (chewing or sucking), its diet breadth (generalist or specialist), and whether it had evolved with *B. rapa* (Danner *et al.,* 2018). Herbivores often use this information to avoid individual plants with conspecifics, while enemies of herbivores are attracted to these plants. In some instances, different developmental stages of the same herbivore species cause different volatiles to be released, and the number of herbivores is reflected in the quantity of volatile emissions (Shiojiri *et al.,* 2010; Clavijo McCormick *et al.,* 2012). It remains to be determined whether plants use this specific information to adjust their responses to particular herbivore risks. In one of the few studies to examine this question, Moreira *et al.* (2018b) found that the cues emitted by *Baccharis salicifolia* under attack by two aphid species differed and were effective at inducing resistance in neighbours only against the aphid that caused the initial damage.

Volatile cues induced by herbivores also differ depending upon the identity of the plant. For example, different accessions of barley emitted different cues and these varied in their effectiveness at inducing resistance against aphids (Pettersson *et al.,* 1999). Communication between sagebrush individuals was more effective if plants were more closely related and shared the same chemotype (Karban *et al.,* 2013, 2014a). Communication also varied among populations such that bean plants from the same location were most effective at communicating and reducing subsequent damage by herbivores (Moreira *et al.,* 2016). Plant sex may also be important; male *Baccharis salicifolia* plants only responded to other males, whereas females responded to cues from both sexes to induce resistance (Moreira *et al.,* 2018a).

Minimising errors

When a plant expresses traits that are not well matched for defence against the herbivores and pathogens that are attacking it, those consumers are often able to successfully exploit the plant. How do plants make sure that they correctly categorise herbivores and do not incorrectly interpret wind or rain as herbivory? The nature of the cue and the duration of exposure provide information that may be used to discriminate between accurate cues and misleading ones. Many HAMPs, such as those in saliva and oviposition fluids, are not ambiguous; they provide information that identifies herbivory specifically as the source of damage.

In cases where priming is involved, plants must receive at least two cues in succession before inducing (Engelberth *et al.,* 2004; Frost *et al.,* 2007). Plants have the ability to store past information (analogous to memory). Most cases of plant memory are short-lived (hours), although examples spanning several years have been reported (Ruuhola *et al.,* 2007; Karban, 2015). The cues may need to be persistent or repeated to elicit a response. For example, sagebrush induced resistance if it received volatile cues from experimentally clipped neighbours that lasted > 1 h; transient puffs of cues lasting shorter periods of time did not trigger a response (Shiojiri *et al.,* 2012a). *Arabidopsis* plants retained a memory of repeated exposures to cues at concentrations that alone were insufficient to cause a response; the cumulative effects of these repeated cues caused release of putatively defensive green leaf volatiles (Shiojiri *et al.,* 2012b).

Some errors in identifying and responding to threats will have larger fitness consequences than others. Therefore, responses may be triggered most readily against the most dangerous risks (Orrock *et al.,* 2015). For example, when plants were attacked by herbivores but not pathogens, they responded incorrectly to herbivores and mounted inappropriate defences against pathogens instead (e.g. Bruessow *et al.,* 2010; Chung *et al.,* 2013). In these cases, the potential fitness losses caused by pathogens may exceed the risks posed by herbivores so that extra vigilance against pathogens may be warranted. Recent models suggest that plant competition and fitness risks may be more important in shaping induced responses than are physiological costs of the defences (Douma *et al.,* 2017).

Future directions for the study of cues that lead to induced responses

Our understanding of both induced responses to herbivory and cues that trigger those responses has certainly progressed. However, basic questions remain unanswered, some because we lack the tools to ask the questions and some because our attention has been focused elsewhere. In the following, I present the questions that I view as most pressing in sub-areas of this research field. This list of questions is extensive and different researchers will prioritise them differently (Heil, 2014).

Mechanisms, cues, and receptors

Our list of modalities that plants use to acquire environmental information in general, and risk of attack in particular, has been expanding. This has been driven by creative explorations of communication modalities that have previously not been known to be within the repertoire of plants.

We know relatively little about the biologically active cues that plants perceive. This is a difficult problem to solve because plant cues can be complex, and we currently lack an efficient method to assay candidates. For example, the volatile emissions from damaged sagebrush plants contain more than 100 compounds that we can detect. This makes deciphering the language

of communication challenging, because relevant information can potentially involve combinations of these compounds that depend upon their absolute and relative doses (ratios). Entomologists made spectacular progress deciphering the language of insect communication by using electroantennography to assess the ability of insects to perceive and respond to particular compounds. Development of similar tools to assay plant responses would allow us to assess whether plants sense and respond to cues. Electroantennograms work by using insect antennae to convert diverse chemical signals (odours) into a single, easily measured, electrical output; this output indicates that the insect has the potential to detect a particular odour. Plants also respond to wounding and other cues of risk by producing electrical signals that propagate systemically and can be detected accurately (Stahlberg *et al.,* 2006; Mousavi *et al.,* 2013; Nguyen *et al.,* 2018). It may be possible to use these electrical signals to evaluate the specific cues that plants perceive.

Another urgent deficiency is our lack of knowledge of the plant receptors of cues about herbivore risk with a few notable exceptions [receptors for elicitors in caterpillar regurgitant and saliva (Truitt *et al.,* 2004, Yamaguchi *et al.,* 2011), receptors for extracellular ATP leaking from ruptured plant cells (Choi *et al.,* 2014), and receptors for ethylene associated with damaged tissue (Hua & Meyerowitz, 1998)]. Plants may also perceive cues by mechanisms other than traditional receptors, such as feedbacks and metabolic conversion. For example, undamaged tomato plants, without a specific receptor, absorbed a volatile green leaf alcohol emitted by damaged neighbours and converted that cue into a glycoside that provided induced resistance against caterpillars (Sugimoto *et al.,* 2014). Identifying plant receptors will move us closer towards understanding plant perception, mechanisms used by herbivores to influence plant responses, and how we can manipulate plant responses in agriculture (Acevedo *et al.,* 2015).

Evolution of plant perception and response

We now know about the biosynthesis of many of the cues that plants perceive but much less about their evolutionary and ecological consequences. The benefits and costs of perceiving and responding to cues are poorly understood. These questions will be best answered in the field, where the selective environment and conditions are more likely to be realistic.

The fitness consequences of responding to cues of herbivory have rarely been examined. What are the benefits of responding to various cues of damage? Are these benefits influenced by the nature of the cue? A modern comparative approach may be useful to understand which species respond and under what conditions. How do the benefits of perceiving and responding to cues vary with plant life history, environmental conditions, and cue reliability? Are cues from some individual plants more reliable than others? What are the ecological and allocation costs of responding to cues? How often and under what conditions are cues honest? Can herbivores, microbes, and other organisms influence these benefits and costs?

We know even less about the consequences of emitting cues than about the response to them. What are the costs and benefits of emitting cues? What tissues, conspecific individuals, or other species perceive cues of damage? Can emission be controlled or targeted to make the information more private? Do cues leak out as an unintended consequence of damage, or is emission an active process?

Ecology

Although the first reports of induced resistance against herbivores appeared roughly 50 years ago, widespread acceptance of this phenomenon by the scientific community only occurred more recently. We continue to discover new forms of information that plants use, although our understanding of the basic natural history of plant perception is still primitive.

The questions listed in the preceding section considered the consequences from the point of view of the plants that emit and respond to cues about herbivory. We know a little more about the effects of induced resistance on herbivore behaviour, growth, survival, and reproductive success, but these topics deserve further attention. Beyond simply demonstrating that induced resistance can affect herbivores, how important is it relative to other factors that also influence them? Can it drive herbivore dynamics or is it a phenomenon that clever experiments can demonstrate but one that has little actual effect on abundance or distribution (see Arimura & Pearse, 2017)?

It goes without saying that plants and particular herbivores are embedded in larger communities. We often study pairs of species or simplified subwebs because the complexity of actual communities and interaction webs is daunting; we assume that we can scale up from what we learn about interactions between pairs of species. We have begun to address these questions, but we should continue to expand our research efforts to more realistic scales. Do examples of communication that have been documented under laboratory conditions translate to the field? We also know that species interactions tend to be highly context-dependent. Are plant perception and response dependent on environmental conditions and other community members?

Agriculture

A natural extension of work on the ecology and evolution of induced responses would involve using our knowledge about how plants naturally regulate their defences to control host plant resistance in agriculture and reduce losses to herbivores. The potential for induced resistance to be a useful tool in agriculture was recognised early on, although efforts have been focused on using herbivore-induced plant cues to manipulate the predators and parasitoids of herbivores rather than host plant resistance (Stenberg *et al.,* 2015; Pickett & Khan, 2016; Turlings & Erb, 2018). The most successful use of volatile cues to date is the 'push–pull' system used by many farmers in Africa to protect maize and other crops (Pickett & Khan, 2016). This system consists of intercropped rows of the valuable crop with another species that emits cues that repel the herbivores, 'pushing' them away from the crop. A third species is planted along the edges of the field that attracts herbivores, 'pulling' them out of the field and away from the crop.

Host plant resistance has received less attention than indirect defences among researchers interested in developing integrated pest management. More direct defences such as induced plant resistance have fewer 'moving parts' than those involving additional trophic levels which may also be dependent on critical nutritional resources, habitat requirements, and so on for predators and parasites.

Can we use elicitors, such as jasmonates (cues that coordinate defences against herbivores by many plants; Howe & Jander, 2008), to manipulate levels of resistance or to prime plants when we anticipate increased risk? Can crop breeding programs increase the emission and/or responsiveness of agricultural cultivars to environmental cues indicating herbivore risk? It has been argued that costs of resistance often involve trade-offs with overtopping growth (Denison, 2012). Selection favours overtopping growth in wild plants that compete with neighbours for light. However, overtopping growth is of no value for agricultural crops that are grown in monocultures. It may be possible to decouple defensive responses from reductions in plant growth and thereby increase yields (Guo *et al.,* 2018).

In addition to crop protection, elicitors or cultural techniques affect crop quality. Grape growers stress their vines to improve wine flavour (including applications of methyl jasmonate) and tobacco growers 'top' plants to increase nicotine. The quality of many crops depends on inducible secondary metabolites and it may be possible to manipulate these to enhance their value (Wüest, 2018).

Conclusions

Relatively little attention has been given to evolutionary and ecological aspects of induced resistance against herbivores. Responses of plants to cues of risk, including induced resistance, have thus far produced few useful solutions to applied problems. While an understanding at biochemical and physiological levels will surely aid such efforts, the current, nearly exclusive, bias towards mechanisms may not be the most effective research strategy. Focusing on phenomenological aspects of induced resistance and plant behaviour will provide us with opportunities for significant progress towards understanding real-world complexity and agricultural applications.

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